*moffatii* Eastw. Perhaps the least that can be said for them is that they help to emphasize more strongly the relation between the sections *Aurator* and *Ericopsis,* a point which was elucidated by Keck.

Colorado College,
Colorado Springs, Colorado

Literature Cited

Keck, D. D. 1937. Studies in Penstemon IV. The Section Ericopsis. Bull. Torrey Club 64:357–381.

Pennell, F. W. 1935. The Scrophulariaceae of eastern temperate North America. Monog. Acad. Phila. 1:i-xiv, 1–650.

Williams, L. 1934. Field and herbarium studies, III. Ann. Mo. Bot. Gard. 21:345–346.

## PECULIARITIES OF THE COLUMBIA RIVER GORGE FLORA

LeRoy E. Detling

The gorge cut through the Cascade Range by the Columbia River as it flows westward between Washington and Oregon has long been recognized as a place of peculiar botanical interest. If one studies the distribution of the plant species found there, he is soon impressed by the large number that are either endemic to the area or occur as isolated populations significantly removed from their normal range. My interest in the history of the various elements of the Pacific Northwest flora led me to speculate upon the meaning of these peculiar distributional patterns. It seemed possible that an analysis of them might furnish clues to the rôle the Columbia Gorge has played in the migrations of vegetation in the past. Its physiography and geographical relationship to adjacent vegetation areas would in themselves lead one to believe that it might have served as a pathway for the migration of many types of organisms. With this in mind, I have spent considerable time during the past few summers studying the local distribution of those plant species occurring within the Gorge. This field work has subsequently been supplemented with herbarium studies on their wider distribution. The present paper is the result of this work.

The species listed herein by no means constitute a complete flora of the Columbia Gorge, although I have tried to make the lists as inclusive as possible. The collections of other botanists who have collected extensively here have also been studied, particularly those of Howell, Gorman, Henderson, Suksdorf, and Sheldon. Nevertheless, further search would undoubtedly reveal more species which might be included in the roster. However, I am confident that the list is sufficiently extensive to give us a good general picture of the significant features of the Gorge flora as a whole, its distribution in the various habitats, and its relation to outside populations, which was the chief purpose of this investigation. Any additions to the number of species will not increase the accuracy of a study made from this particular viewpoint.

## Physiography and Climate of the Gorge

The Cascade Range has been formed by a combination of gradual uplift since the Miocene epoch and of volcanic action largely during the Pliocene and Pleistocene. During this process the Columbia River, without materially altering its course, kept pace with the change by cutting its bed deeper and deeper, thus forming the great gash through the mountains which we know as the Columbia River Gap, or in a more restricted sense the Columbia River Gorge. Lateral erosion has been much slower than that carried on by the main stream, resulting in a deep canyon with precipitous walls, extending for some thirty-five miles. The small streams which flow into the river have cut their beds back into this canyon wall sometimes as much as a half mile, forming deep, narrow, lateral gorges into which the streams frequently plunge as waterfalls from a hundred to several hundred feet high.

Erosion has been less effective on the south wall of the canyon than on the north, and it is here that the most spectacular cliffs are to be seen. One of the most striking of these is the north face of St. Peter's Dome, which rises abruptly for about twenty-five hundred feet. Some of the cliffs have their bases almost at the river's edge, while others rise as much as a half mile or more back from the water. On the north wall of the Gorge the bases of the sheer drops are usually farther back from the river as well as higher up. A noticeable feature of both walls of the canyon is the frequent stair-step arrangement, apparently due to differences in hardness of the various strata of rock. It is of interest, but perhaps of no further consequence to us, that these steps, and therefore the shelves upon which much of the vegetation is growing, are roughly about six hundred feet one above the other. Thus there are a number of places where a shelf occurs about six hundred feet above the river, with other shelves above this at elevations of approximately twelve hundred and eighteen hundred feet. At most places the eighteen-hundred-foot shelf marks the top of the most abrupt cliffs, and the rise above that, while steep, is nevertheless a distinct slope, usually forested.

For an area so limited in extent the Columbia Gorge has an extremely varied climate. This is due in part to the depth of the canyon itself, in part to the influence of two entirely different climates at either end of the canyon, and in part to the general east-west orientation of the gap.

The curve of annual precipitation through the Gorge follows rather closely that of any transect extending from the Willamette Valley eastward across the Cascade Range to the central Oregon plateau. Although the level of the river bed rises comparatively little as one follows it eastward through the canyon, yet the elevation of the mountains that press in on either side is such as to raise the moisture-laden air masses from the Pacific Ocean sufficiently to cause a heavy precipitation over the central sector of the Gorge. The mean annual precipitation at Vancouver of 37 inches is typical for points along the lower Willamette and Columbia rivers. However, at Mount Pleasant, situated close to the western portal of

the Gorge, this figure has risen to 57 inches. Rainfall increases eastward to the vicinity of Cascade Locks where an average of approximately 75 inches is measured. Upstream from here there is a sharp drop in the annual mean. At Hood River and White Salmon about 30 inches are recorded, and at Lyle 25 inches.

Recorded data on temperatures in the Gorge do not tell us a great deal. Between Mount Pleasant and Hood River there is a gradual drop of 4.7°F. in the mean January temperature. In the same distance the mean July temperature rises 2.3°F.

One striking feature of the Gorge climate does not appear in the records. When atmospheric pressure differentials are favorable, masses of air move from eastern Oregon and Washington westward through the Gorge. In winter this situation frequently results in cold winds which at times reach very high velocities. When this occurs in conjunction with rainfall the result is often a very serious "silver thaw," i.e., a rain which freezes as it touches the ground, or trees and other vegetation. These freezing rains sometimes last for several days, and the breakage of trees and destruction of other types of plant life may be quite serious. A parallel situation frequently occurs during the summer when hot, dry east winds blow down through the gap, sometimes for several days at a time. The effect that such winds might have upon the vegetation is obvious.

As might be expected in a canyon with an east-west orientation, the local climate of the north wall is quite different from that of the south wall. This is clearly reflected in the difference in the general vegetation of the two sides. The flora of the dry, warm area of central Oregon and Washington extends much farther westward on the well-insolated south-facing slopes than on the north-facing wall, which is in deep shadow much of the time. One the other hand, the Douglas fir forest and its associates follow the cool north-facing slopes entirely through the Gorge to the Hood River Valley.

The significance of the Columbia Gap from the standpoint of such a climatic and vegetational barrier as the Cascade Range may be realized when we recall that it is the only point between the Fraser River in British Columbia and the Klamath River in northern California where the axis of the range has been cut through in such a way as to interrupt the continuity of all the life zones above the Transition. In this case the cutting has extended almost to sea level.

## Flora of the Gorge

To understand fully the flora of the Gorge and the implications of the distribution patterns of many of its species we must look first at the type of vegetation now existing in the adjacent lowlands at either end.

To the west the Gorge opens out upon what I have elsewhere called the Puget Area (Detling, 1948). This vegetation area occupies the broad valley between the Cascades and the Coast Range, extending from the south-

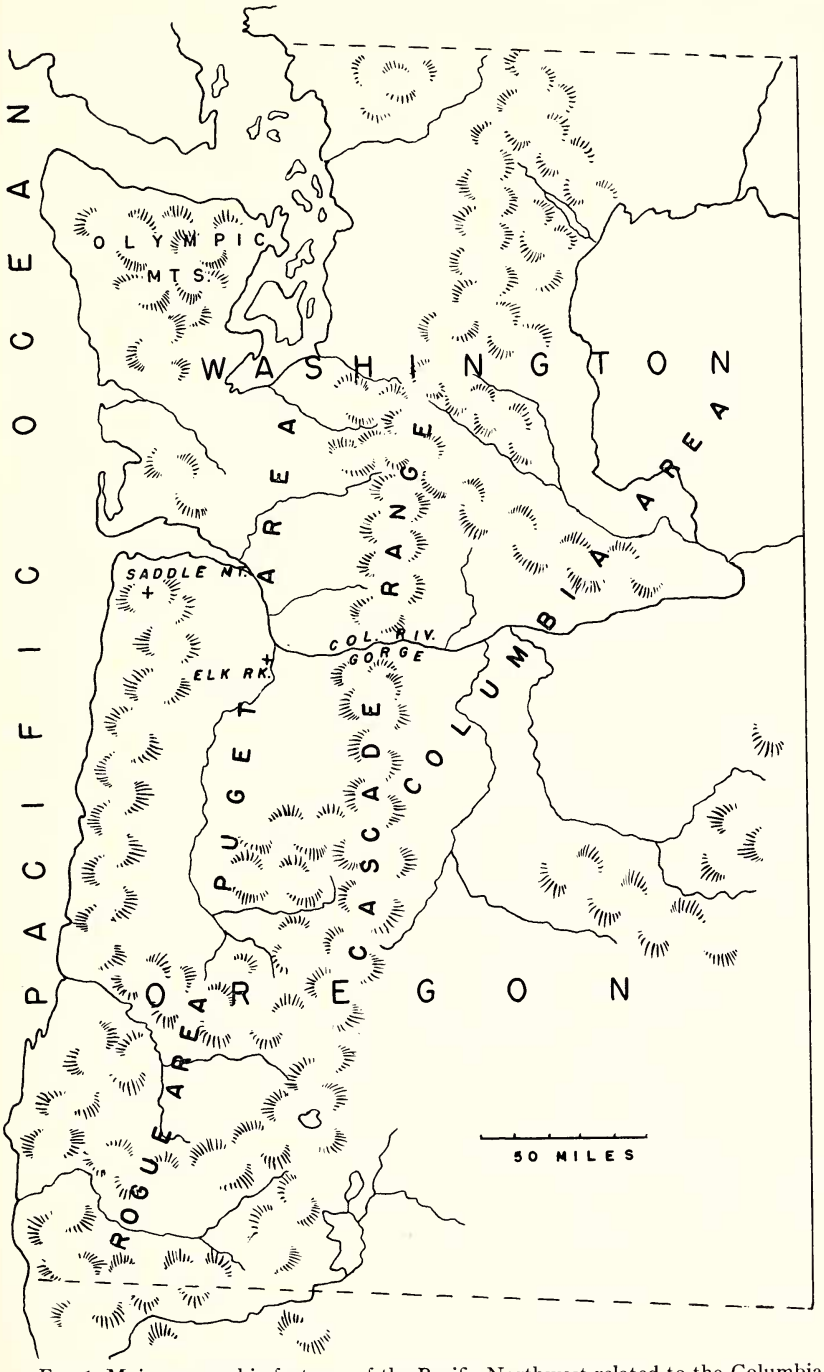


FIG. 1. Main geographic features of the Pacific Northwest related to the Columbia Gorge flora.

ern limits of the Willamette watershed in Oregon northward to Puget Sound and southern British Columbia. From a physiographic standpoint it coincides more or less with what the geomorphologists call the Puget Trough. The vegetation of the area is basically a Douglas fir forest, with an intermingling of oak-madrone woodland and grassland at lower levels and on the valley floor. Annual precipitation is high and neither summer nor winter temperatures are extreme. These conditions result in a dense forest cover, especially in the foothills, with an understory of vine maple (*Acer circinatum*), salal (*Gaultheria shallon*), low Oregon grape (*Mahonia nervosa*), and red huckleberry (*Vaccinium parvifolium*), along with a wealth of herbaceous species.

Eastward the Gorge widens out and merges with the Columbia Area, again to use a name adopted by the author (op. cit.). This area occupies the valley of the Columbia River in north-central Oregon and south-central Washington, and such tributary valleys as those of the Yakima, John Day, and lower Deschutes rivers. The Hood River Valley comprises its westernmost extension. Annual precipitation is light throughout the area (13 inches at The Dalles). Winter temperatures are frequently very low, while the summers are hot. Apparently the region was originally a grassland, but there has been an invasion of sagebrush (*Artemisia* species) where the land has been overgrazed. Stands of ponderosa pine (*Pinus ponderosa*) are not uncommon on the hills where soil, moisture, and temperature conditions are favorable.

1. Species of wide distribution. For purposes of analysis I have found it convenient and useful to divide the Columbia Gorge species into groups according to their present general distribution. The first of these comprises a relatively large number of species (70, which is 34.0 per cent of the total of 206) which are widely distributed and occur at lower and middle elevations on both sides of the Cascade Range. From the standpoint of their origin this group can be divided again into two sub-groups —one whose members have probably come into our region from the north, the other evidently having originated to the south. In trying to determine where any given species has originated we may use several criteria. It is admitted that the use of any of these criteria alone would be unsound, but when they lend mutual support, and especially when applied to relatively recent migrations (from the standpoint of geological time), they probably present a fairly accurate idea of the direction of migration of most of the components of this flora. The criteria that seem most applicable to the problem at hand are: (a) The present maximum concentration of individuals of a species is likely to be somewhere near the area from which it has radiated in its migrations, and such concentration will probably be found in environmental conditions similar to those under which it originated. (b) A species is more likely to have come from a region where obviously close relatives are now located, than from a region in which such relatives are absent. (c) When a species typically occurs as a member of a definite species association, the area of origin of whose other

members can be postulated, we may assume it is safe to assign to it that same origin.

Judged on these bases the northern element of this first group consists of those species whose centers of distribution are to the north of the Columbia River; their present range frequently extends as far north as Alaska. At our latitude they are plants of shaded woodlands and stream banks, mostly associates of the coniferous forests. As might be expected from the dryness and high summer temperatures of the Columbia and Deschutes areas, the species tend to be absent from these two areas, but are common in the foothills and lower mountain slopes west of the Cascade crest and again in the Blue Mountains and in the Rocky Mountains of Idaho and Montana. It is highly probable that most of them migrated into our region by following the Cascade and Rocky Mountain ranges southward. The following species make up this sub-group:

Adiantum pedatum L.
  var. aleuticum Rupr.
Aquilegia formosa Fisch.
Cerastium arvense L.
Chimaphila menziesii (R.Br.) Spreng.
Chimaphila umbellata (L.) Nutt.
  var. occidentalis (Rydb.) Blake
Circaea pacifica Asch. & Mag.
Cirsium edule Nutt.
Clintonia uniflora (Schult.) Kunth.
Cornus stolonifera Michx.
Elymus glaucus Buckl.
Epilobium angustifolium L.
Festuca occidentalis Hook.
Festuca rubra L.
Festuca subulata Trin.
Galium aparine L.
Geranium bicknellii Britt.
Heracleum lanatum Michx.
Heuchera micrantha Dougl.
  var. pacifica R.B.L.
Linnaea borealis L.
  var. americana (Forbes) Rehd.
Lupinus polyphyllus Lindl.
Lupinus rivularis Dougl.
Melica subulata (Griseb.) Scribn.
Mimulus guttatus DC.
Physocarpus capitatus (Pursh) Ktze.
Poa gracillima Vasey
Poa nervosa (Hook.) Vasey
Potentilla glandulosa Lindl.
Pseudotsuga menziesii (Mirb.) Franco
Pteridium aquilinum (L.) Kuhn
  var. pubescens Underw.
Rosa gymnocarpa Nutt.
Rosa nutkana Presl
Rubus parviflorus Nutt.
Sambucus glauca Nutt.
Sedum spathulifolium Hook.
Selaginella douglasii (Hook. & Grev.)
    Spring.
Sisyrinchium idahoense Bickn.
Smilacina racemosa (L.) Desf.
Smilacina sessilifolia (Baker) Nutt.
Symphoricarpos albus (L.) Blake
Thalictrum occidentale Gray
Thuja plicata Donn.
Tiarella unifoliata Hook.
Trientalis latifolia Hook.
Trillium ovatum Pursh
Viola glabella Nutt.

The species comprising the southern element of this first group have their present centers of distribution to the south of the Columbia River. None extends as far north as Alaska, although some reach southern British Columbia in the dry region east of the Cascades. West of the mountains they are most typically associated with the oak-madrone woodland, and when they occur at middle and higher elevations it is on exposed places with shallow soil, strong insolation, or other factors favoring a xeric flora. The members of this sub-group display less tendency to avoid the Columbia and Deschutes areas. They have probably arrived at our lati-

tude by way of the system of valleys west of the Cascades or by way of the valleys and plateaus adjacent to the Great Basin east of this range.

Adenocaulon bicolor Hook.
Allium acuminatum Hook.
Amelanchier florida Lindl.
Apocynum pumilum (Gray) Greene
Asarum caudatum Lindl.
Bromus vulgaris (Hook.) Shear
Castilleja hispida Benth.
  var. hispida
Crocidium multicaule Hook.
Cryptantha hendersonii (Nels.) Piper
Delphinium menziesii DC.
Eriophyllum lanatum (Pursh) Forbes
Erysimum capitatum (Dougl.) Greene
Gilia capitata Hook.
Holodiscus discolor (Pursh) Maxim.
Koeleria cristata (L.) Pers.
Lilium columbianum Hans.
Lotus douglasii Greene
Madia gracilis (Smith) Keck
Microsteris gracilis (Dougl.) Greene
Pinus ponderosa Dougl.
Prunus demissa (Nutt.) Dietr.
Rhamnus purshiana DC.
Sedum douglasii Hook.
Trifolium microcephalum Pursh
Zygadenus venenosus Wats.

2. Puget Area element. Another large group of species represented in the Gorge (54 in number and 26.2 per cent of the total) differs from the previously listed one in being restricted to the west side of the Cascade axis. They are, for the most part, common and widely distributed in the Puget Area and form a considerable part of its basic flora.

Acer circinatum Pursh
Acer macrophyllum Pursh
Achlys triphylla (Smith) DC.
Alnus oregona Nutt.
Anemone deltoidea Hook.
Arnica amplexicaulis Nutt.
Aruncus silvester Kostel.
  var. acuminatus (Dougl.) Jepson
Asplenium trichomanes L.
Brodiaea coronaria (Salisb.) Engler
Campanula scouleri Hook.
Cimicifuga elata Nutt.
Cornus nuttallii Aud.
Corydalis scouleri Hook.
Corylus californica (A. DC.) Rose
Delphinum oreganum How.
Dicentra formosa (Andr.) DC.
Dryopteris arguta (Kaulf.) Watt.
Fragaria bracteata Hel.
Gaultheria shallon Pursh
Hydrophyllum tenuipes Hel.
Iris tenax Dougl.
Mahonia aquifolium (Pursh) Nutt.
Mahonia nervosa (Pursh) Nutt.
Maianthemum bifolium DC.
  var. kamtschaticum (Gmel.) Jeps.
Melica harfordii Boland.
Montia parvifolia (Moc.) Greene
Oplopanax horridum (Sm.) Miq.
Oxalis oregana Nutt.
Oxalis trilliifolia Hook.
Penstemon ovatus Dougl.
Penstemon serrulatus Menz.
Phacelia nemoralis Greene
Philadelphus lewisii Pursh
  var. gordonianus (Lindl.) Jeps.
Plectritis congesta (Lindl.) DC .
Polypodium vulgare L.
  var. occidentale Hook.
Polystichum munitum (Kaulf.) Presl
Prunus emarginata (Dougl.) Walp.
  var. mollis (Dougl.) Brew.
Pyrola bracteata Hook.
Rhododendron macrophyllum D. Don.
Rhus diversiloba T. & G.
Ribes bracteosum Dougl.
Ribes sanguineum Pursh
Romanzoffia suksdorfii Greene
Rubus spectabilis Pursh
Sambucus callicarpa Greene
Stachys emersonii Piper
Struthiopteris spicant (L.) Weis.
Tellima grandiflora (Pursh) Dougl.
Tiarella trifoliata L.
Tolmiea menziesii (Pursh) T. & G.
Tsuga heterophylla (Raf.) Sarg.
Vaccinium parvifolium Smith
Valeriana sitchensis Bong.
  var. scouleri (Rydb.) Piper
Vancouveria hexandra (Hook.) Morr. & Dcne.

3. Columbia Area element. These species (27 in number, 13.2 per cent of the total) are typical members of the plant associations found in the Columbia Area, at least in its western portion, i.e., near the upper end of the Gorge. Some of them range beyond the confines of the area, occurring at relatively low elevations and in situations ecologically similar to those in the Columbia Area. When these occur west of the Cascades it is normally in the Rogue River Valley and southward, but not in the Puget Area.

*Anemone oregana Gray
Arnica cordifolia Hook.
Bromus tectorum L.
Castilleja hispida Benth.
var. acuta Penn.
*Crepis barbigera Leib.
Dicentra cucullaria (L.) Bernh.
var. occidentalis (Rydb.) Peck
*Dodecatheon poeticum Hend.
Eriogonum sphaerocephalum Benth.
var. tenue (Small) Piper
Hackelia diffusa (Lehm.) Johnst.
Helianthus cusickii Gray
*Hydrophyllum capitatum Dougl.
var. thompsonii (Peck) Const.
Iliamna rivularis (Dougl.) Greene
Lewisia rediviva Pursh
Luina nardosmia (Gray) Cronq.
var. glabrata (Piper) Cronq.
*Lupinus leucopsis Agardh
var. bingensis (Suks.) C. P. Sm.
Microseris nutans (Geyer) Schultz-Bip.
*Penstemon barrettae Gray
Penstemon richardsonii Dougl.
Penstemon subserratus Penn.
Philadelphus lewisii Pursh
var. lewisii
Phlox speciosa Pursh
Poa ampla Merr.
Prunus emarginata (Dougl.) Walp.
var. emarginata
Senecio integerrimus Nutt.
var. exaltatus (Nutt.) Cronq.
Silene douglasii Hook.
Spiraea lucida Dougl.
Trifolium macrocephalum (Pursh) Poir.

The six species preceded by an asterisk are of especial interest in that they occupy a very restricted region. They have their centers of distribution near the east end of the Gorge and are strictly endemic to this part of the Columbia Area. In the Gorge they usually occur toward the east end and, as might be expected, in fairly dry situations. Since the *Lupinus* and *Penstemon* species referred to here do not actually occur west of Mosier, it is doubtful whether they should be considered in our discussion of the Gorge flora. I list them merely because they form part of a flora which does have a definite relationship to the Gorge.

4. Rogue Area element. A significant element of the Columbia Gorge flora (17 species, or 8.3 per cent) is typically associated with the oak-madrone woodland of the Rogue Area of southwestern Oregon (op. cit.), its components having their centers of distribution either there or farther to the south. However, they occur again rather frequently in the Columbia Area, especially in that portion near the upper end of the Gorge. These species rarely occur otherwise east of the Cascades. In the Puget Area they commonly appear as components of some rather striking islands of xeric vegetation growing on exposed rocky points in the Douglas fir belt (Detling, 1953). Their peculiar distribution pattern suggests the probability that during a warm, dry period they migrated northward from the

Rogue into the Puget Area, then eastward through the Columbia Gorge into the Columbia Area. During a succeeding cooler and moister phase of the climatic cycle these species have been much restricted in their occurrence in the Puget Area, and probably in the Gorge and in the Columbia Area as well.

Balsamorhiza deltoidea Nutt.
Collinsia grandiflora Dougl.
Collinsia parviflora Dougl.
Comandra umbellata (L.) Nutt.
Dichelostemma pulchellum (Salisb.) Hel.
Eriogonum compositum Dougl. var. pilicaule St. J. & War.
Godetia amoena Lilja
Godetia quadrivulnera (Dougl.) Spach
Leptotaenia dissecta Nutt.
Lotus micranthus Benth.
Lupinus bicolor Lindl.
Lupinus laxiflorus Dougl.
Phacelia linearis (Pursh) Holz.
Quercus garryana Dougl.
Senecio harfordii Greenm.
Triteleia grandiflora Lindl. var. howellii (Wats.) Hoover
Viburnum ellipticum Hook.

5. Boreal element. A group of 31 species (15.1 per cent of the total) occurs normally at fairly high elevations in the Cascades, but is of interest here because its members are found rather abundantly at or near the bottom of the Gorge. Typically Canadian or Hudsonian Zone species, they usually range above 4000 feet. Some of them occur only in the Cascades, while others are found also in the mountain ranges both to the west and to the east of the Cascade axis; however, with only two or three exceptions they do not descend to the valley and plateau levels on either side. In the Gorge these species are nearly always found below the 1600-foot level, i.e., they are limited largely to the steep bluffs and cool lateral canyons, mostly on the south side of the river. In each case they are isolated from the main body of the population by a broad band of forested and less precipitous terrain in which I have so far found no record of their occurrence.

*Acer glabrum Torr. subsp. douglasii (Hook.) Wesml.
*Alnus sinuata (Regel) Rydb.
*Antennaria racemosa Hook.
Arabis furcata Wats.
Arctostaphylos uva-ursi (L.) Spreng.
Arnica discoidea Benth. var. eradiata (Gray) Cronq.
*Campanula petiolata DC.
Cornus canadensis L.
Cryptogramma acrostichoides R. Br.
Dodecatheon dentatum Hook.
Dryopteris linnaeana C. Chr.
Habenaria unalaschensis (Spreng.) Wats.
Haplopappus hallii Gray
Lewisia columbiana (How.) Robins.
*Lomatium angustatum (C. & R.) St. John
Menziesia ferruginea Hook. var. glabella (Gray) Peck
Mitella trifida Graham
Penstemon nemorosus (Dougl.) Trautv.
Penstemon rupicola (Piper) How.
*Phlox diffusa Benth. subsp. longistylis Wherry
Polemonium carneum Gray
*Polypodium vulgare L. var. columbianum Gilb.
Populus tremuloides Michx.
*Saxifraga bronchialis L. var. vespertina (Small) Rosend.
*Saxifraga caespitosa L.
Saxifraga rufidula (Small) Macoun
*Stenanthium occidentale Gray
Suksdorfia violacea Gray
Trautvetteria grandis Nutt.
Vaccinium membranceum Dougl.
Woodsia scopulina D. C. Eaton

Ten species of the foregoing list (designated by asterisks) constitute an interesting group because of their relationship to the flora of Saddle Mountain. This peak is located in Clatsop County, Oregon, about 75 miles northwest of the western portal of the Gorge. Although only slightly over 3200 feet in elevation, it is the site of an isolated boreal flora which it may be assumed was at one time continuous with that now found in the Olympic Mountains (Detling, 1954). At the present time this flora has been eliminated from the areas between Saddle Mountain and the Olympics, and occurs only occasionally southward in the Oregon Coast Range, e.g., on Marys Peak. The ten indicated Columbia Gorge species have this peculiar and interesting distribution, occurring also on Saddle Mountain and in the Olympics, but so far as we know not between these points.

6. Endemic species. Of the 206 species considered here as representing the flora of the Columbia Gorge, seven are endemic to the Gorge:

Bolandra oregana Wats.
Douglasia laevigata Gray var. laevigata
Erigeron howellii Gray
Erigeron oreganus Gray
Hieracium longiberbe How.
Sullivantia oregana Wats.
Synthyris stellata Penn.

It is true that two of those included in this category, *Bolandra oregana* and *Sullivantia oregana,* have been found at one other station outside the Gorge, namely at Elk Rock on the lower Willamette River, and thus are not truly endemic to the Gorge and in the strictest sense of the term; however, they must be considered here in any discussion of endemism as it relates to the history of the flora.

Elk Rock is a sheer cliff on the west bank of the Willamette River a few miles above Portland and twenty-two miles by air from the west portal of the Gorge at Crown Point. The face of the bluff has an easterly and slightly northerly exposure; in certain spots seepage water keeps the surface wet most of the time. Apparently conditions here are sufficiently similar to those in certain niches of the Gorge to have encouraged the persistence of a few rare plant species which are otherwise found only in the cool, misty vicinity of the waterfalls of the Gorge. This situation suggests that during some period of glaciation in the Northwest the cold was intense enough to cause the extension of the boreal flora from the Cascades out over the valley floor at least as far as the Willamette River.

There are two possibilities always to be considered regarding the origin of narrowly endemic species. In the first place, they may be of relatively recent origin, having risen through mutation or hybridization from some pre-existing species in the area they now occupy. Theoretically, given time and proper environmental conditions, such a species would be expected to increase in number of individuals and to extend into nearby territory. On the other hand, endemic populations may be relicts of species which once were more widely distributed, but which, due to some factor such as failure to cope with a changing environment have been reduced to their present limited range.

Viewed as a whole, the endemic species of the Gorge would seem to be of the latter type. This conclusion is based upon the occurrence of two of them isolated at Elk Rock, upon the fact that they seem to be morphologically stable and not undergoing further evolutionary development, and finally that for the most part they have no near relatives in the vicinity.

These seven species are well-defined entities, and the plant taxonomist has no difficulty in placing them in the category of "endemics." However, when one studies carefully the wide-ranging species represented in the Columbia Gorge his attention is soon called to the fact that evolutionary processes have frequently taken place in the Gorge, and presumably are still going on, which have made that portion of the species slightly, but still noticeably, different morphologically from the rest of the population. Specialists in certain groups have already called attention to some of these, e.g., Cronquist (1955) for *Arnica amplexicaulis* and *Haplopappus hallii,* but they are frequently loath to give such local forms taxonomic standing. However, we cannot ignore the fact that they are there, and if we wished to follow the lead of less conservative botanists and give varietal or subspecific names to these local entities we could increase considerably the number of endemics in our list. These would of course be of the first type as to origin.

## General Discussion

Viewed from the standpoint of the major migrations of the Pacific Northwest flora, there are two outstanding phases in which the geographical situation, physiographic features, and structure of the vegetation of the Columbia River Gorge are probably significant.

The first of these is the rôle of the Gorge as a gateway for the passage of lowland species from one side of the Cascade axis to the other. For the rather large number of species (81, or 39.4 per cent) now confined to one side or the other of the axis, the Gorge obviously has not fulfilled this function. Even among the 70 species with a general distribution both east and west it is unlikely that many have migrated through the Gorge. Judging from their present widespread occurrence they probably reached the vicinity of the Gorge by parallelling the range on either side.

There is evidence, however, that a significant number of lowland species from other groups listed above have migrated through the Gorge in assuming their present distribution. Chief among these are the Rogue Area species found in the Columbia Area, with their isolated occurrences in xeric islands west of the Cascades. It was inferred in the earlier brief discussion of this group that the migration of its members through the Columbia Gorge took place from west to east. The basis for this inference is the fact that the centers of distribution of these species are to the south and west today, and any evidence of former occurrence is now found west of the Cascades. *Quercus garryana* may be cited as an example. This migration probably took place at a time of maximum northward extension of the Rogue flora. Floral migrations from an areal center normally occur

while climatic conditions at the center are becoming intensified and the environment in advance of the migration is becoming progressively more like that of the center. Since essentially the Rogue Area center is relatively warm and dry, the northward extension of the Rogue flora probably coincided with a xerothermic phase in the climatic cycle of the Pacific Northwest. Studies on post-glacial forest succession in the Northwest, based upon pollen profiles from peat bogs (Hansen, 1955), indicate that such a warm, dry phase did set in approximately 8000 years ago and lasted until about 4000 year ago, with its maximum probably about 6500 years from the present.

The other distinctive feature of the Gorge flora is the fact that such a large part of it constitutes an island of boreal forms isolated at the bottom of the main canyon or its smaller tributary canyons. These are in all probability relict occurrences, left from a time when the boreal flora, pushed to lower levels from above, was continuous from the middle mountain elevations down to the present valley level. It is hard to conceive that such a large number of species would have been established at their present levels by being transported from higher elevations across a transitional zone during a period of temperate climate. Rather, it is more likely that there was a general downward shifting of the flora during a cold phase of the climatic cycle, and subsequent isolation of many of the species in favorable niches as the climate became warmer and the main populations of the boreal species retreated to higher elevations. The presence of a number of Columbia Gorge species on Saddle Mountain and in the Olympics is another indication of a former continuity of the boreal flora at low levels in this part of the Pacific Northwest.

The narrow endemics briefly discussed above were probably reduced to their present restricted range during or following the culmination of this cold maximum. The occurrence of some of these isolated along the lower Willamette River may indicate that at one period their range at valley level was considerably more extensive.

The cold maximum which caused the downward migration of the boreal species must have preceded the warm, dry phase of climate previously mentioned, as the pollen profiles indicate only moderate cooling in the last 6000 years. These same profiles, correlated with radiocarbon datings (Broecker, Kulp, and Tucek, 1956), indicate that the last major cold maximum in this part of the continent occurred about 12,000 years ago, a time probably coinciding with the maximum advance of the last continental ice sheet in western North America.

Museum of Natural History
University of Oregon, Eugene

## Literature Cited

Broecker, W. S., J. L. Kulp, and C. S. Tucek. 1956. Lamont natural radiocarbon measurements. III. Science 124:154–165.

Cronquist, Arthur. 1955. Compositae, *in* C. Leo Hitchcock, Arthur Cronquist, Marion Ownbey, and J. W. Thompson, Vascular plants of the Pacific Northwest, Part 5. Univ. of Washington Press, Seattle.

Detling, LeRoy E. 1948. Concentration of environmental extremes as the basis for vegetation areas. Madroño 9:169–185.

———. 1953. Relict islands of xeric flora west of the Cascade Mountains in Oregon. Madroño 12:39–47.

———. 1954. Significant features of the flora of Saddle Mountain, Clatsop County, Oregon. Northwest Science 28:52–60.

Hansen, Henry P. 1955. Postglacial forests in south-central and central British Columbia. Am. Jour. Sci. 253:640–658.

## THE GENUS COLLINSIA. III. THE SIGNIFICANCE OF CHIASMATA FREQUENCIES AS A CYTOTAXONOMIC TOOL[1]

E. D. Garber

The genus *Collinsia* Nutt. (Scrophulariaceae) includes twenty-one recognized species, divided into two groups (Newsom, 1929; Pennell, 1951). The species in one group have "sessile" flowers congested in whorls, with pedicels shorter than to no longer than the calyces of the lower whorls, and with flat, mature seeds. The species in the other group have pedicelled flowers, either solitary or in whorls, with the pedicels of the flowers of the lower whorls from as long as to longer than the calyces, and with either flat or thick, mature seeds. There are other differences between the species in these two groups but they are not as clear as those which have been mentioned. The basic chromosome number for the genus is 7; no polyploid species have yet been found (Garber, 1956, and unpubl.).

The species in each of the two groups apparently differ in their mean number of chiasmata per bivalent at metaphase I. With the exception of *C. corymbosa* Herder, the species with "sessile" flowers have mean values of 1.1–1.5 and the species with pedicelled flowers, 1.7–1.9 (Garber, 1956). *Collinsia corymbosa* was placed in the species group with "sessile" flowers by both Newsom (1929) and Pennell (1951), yet its combination of characters shows it to be somewhat intermediate between these two groups of species (Garber and Gorsic, 1956). The flowers are borne in dense, capitate whorls on pedicels 3–7 mm. long, with calyx lobes approximately 5 mm. long, and the mature seeds are thick. The mean number of chiasmata per bivalent at metaphase I in *C. corymbosa,* however, has been found to be 1.7–1.8, a value characteristic of the group of species with pedicelled flowers.

This paper presents evidence regarding the validity of chiasma frequency as a cytotaxonomic tool in studying relationships among species of *Collinsia* by considering the chromosome associations and aberrations

[1] This investigation was aided by grants from the National Science Foundation and the Dr. Wallace C. and Clara A. Abbott Memorial Fund of The University of Chicago.